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Exotic eucalypts: from demonized trees to allies of tropical forest restoration?

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Abstract:

1. Despite ambitious, international forest landscape restoration targets, few forest restoration approaches provide both ecologically sound and financially-viable solutions for achieving the spatial scale proposed. One potential revenue source for restoration is selective harvesting of timber, a product for which there is a clear global market and increasing demand. Although the use of commercially valuable exotic trees may attract farmers to restoration, it can be a major concern for ecologists.

2. Here, we present results collected over 7 years from experimental studies at three sites across the Brazilian Atlantic Forest to assess the impacts of incorporating exotic eucalypts as a transitional stage in tropical forest restoration on aboveground biomass accumulation, native woody species regeneration, and financial viability. .

3. Biomass accumulation was nine times greater in mixed eucalypt-native species plantations than native only plantings due to fast eucalypt growth. Nonetheless, the growth of native non-pioneer trees was not affected or only slightly reduced by eucalypts prior to logging.

4. Eucalypts did not negatively affect the natural regeneration of native woody species before or after eucalypt logging. Canopy cover regrew quickly but was slightly lower a year following logging in mixed eucalypt-native species plantations. Natural regeneration richness and planted non-pioneer growth were similar across treatments in the post-logging period. We found higher variation of biomass accumulation and native species regeneration among sites than between plantation types within sites.

5. The income obtained from eucalypt wood production offset 44-75% of restoration implementation costs.

6. *Synthesis and applications.* Many of the negative effects attributed to eucalypts on the growth and natural regeneration of native trees depend on features of the production system, landscape structure, soil, and climate in which they are grown, rather than the effects of eucalypts *per se.* In Brazil's Atlantic Forest region, exotic eucalypts can become important allies of tropical forest restoration, and their use and investment opportunities should be considered within the portfolio of options supported by public and private funding and policies.

Keywords: Atlantic Forest; ecological restoration; *Eucalyptus*; forest and landscape restoration; large-scale restoration; natural regeneration; restoration costs; restoration economy; selective harvesting; tropical forestry

Introduction

Tropical forest restoration has emerged as a promising intervention to mitigate climate change, biodiversity loss, and improve human wellbeing in regions of the planet where high endemic species richness coincides with widespread deforestation and forest fragmentation (Holl 2017). Ambitious restoration targets have been set for tens to hundreds of millions of hectares in tropical forest regions at the national, regional, and international scales (e.g. Bonn Challenge, Initiative 20 × 20 in Latin America, Atlantic Forest Restoration Pact in Brazil; Chazdon *et al.* 2017). But the high costs of forest landscape restoration present a major obstacle for widescale adoption. For example, the implementation phase alone can cost upwards of US$3,700 per hectare in Brazil (Molin *et al.* 2018), and international financing for such efforts is limited compared to the large area proposed for restoration (12 M ha in Brazil alone). Restoring tropical forests requires more than just compensating landowners for the use of the land. It demands substantial investments in the implementation, maintenance, and long-term protection and monitoring of recovering forests (Brancalion *et al.* 2017; Reid *et al.* 2018). Hence, tropical countries need to develop innovative, financially-viable approaches to forest restoration that are not heavily dependent on external aid that can stimulate large-scale application to reach scale (Ding *et al.* 2017).

One potential revenue source for restoration is selective harvesting of timber, a product for which there is a clear global market and increasing demand (Putz *et al.* 2012). From an ecological perspective, forest restoration projects should prioritize planting native tree species. However, fast-growing, exotic species comprise a potential alternative, if they can help offset planting costs, do not inhibit the recolonization and growth of native species, and speed up the recovery of forest functions (Ashton *et al.* 1997; Lamb, Erskine & Parrotta 2005; Catterall 2016). Extensive production knowledge and established timber markets for certain exotic tree species may transform restoration plantings into a profitable activity and create investment opportunities (Brancalion *et al.* 2012; Grossman 2015; Payn *et al.* 2015). Several studies have found abundant and diverse regeneration of native woody species in the understory of commercial tree plantations across the global tropics (e.g. Brockerhoff *et al.* 2013; Pryde *et al.* 2015; Wu *et al.* 2015), and highlight the potential of timber plantations to promote large-scale forest restoration (Lugo 1997; Parrotta, Turnbull & Jones 1997). However, we are not aware of any controlled or replicated experiments that rigorously assess the ecological and economic outcomes of interplanting commercial exotic species with a diverse suite of native species to facilitate regeneration of a diversity of tropical forest species and offset restoration implementation costs by harvesting exotic planted trees.

Exotic eucalypts, planted for wood pulp and timber, are ubiquitous in tropical regions, and currently cover over 20 million hectares globally. Only nine out of >700 *Eucalyptus* and *Corymbia* species (hereafter referred to as “eucalypts”) comprise >90% of the global planted area (Stanturf *et al.* 2013). The prominent environmental concerns associated with the large plantation area and ecological characteristics of exotic eucalypts have motivated several studies to assess their biodiversity value, allelopathic effects, water consumption, and potential for invading unplanted areas (Bremer & Farley 2010; Stanturf *et al.* 2013; Becerra *et al.* 2017). The effects of eucalypts vary, however, with regional climate, previous land use, and plantation management practices (Brockerhoff *et al.* 2013).

Eucalypts are grown in Brazil mostly for pulp, but also for round logs, sawn lumber, firewood, fencing poles, and oil (IBA 2018). Such flexible uses and high productivity (Brazil’s average: 35 m^3 ha^{-1} yr^{-1}, but reaching >60 m^3 ha^{-1} yr^{-1} in some regions) make eucalypts popular commercial trees for farmers (Goncalves *et al.* 2013); hence, eucalypts comprise 71% of tree plantation area in Brazil (5.7 Mha, IBA 2018) and are widely used in plantations throughout Latin America (Geary 2001; Salas *et al.* 2016). Most of these plantations have been intensively managed in short rotations (~5 yr) and as extensive monoculture areas, which have prevented the natural regeneration of native woody species and resulted in so-called “green deserts” (Bremer & Farley 2010). However, less intensively managed and abandoned eucalypt plantations in many regions host a high diversity of plants and birds (Silva-Junior, Scarano & Cardel 1995; Marsden, Whiffin & Galetti 2001; Lopes *et al.* 2015; César *et al.* 2017).

Forest restoration projects in Atlantic forest region of Brazil mostly plant a high diversity of native tree species (Rodrigues *et al.* 2011; Brancalion *et al.* 2018), but the Native Vegetation Protection Law of 2012, allows for intercropping exotic, commercially-valuable tree species with native species in restoration projects to meet restoration requirements . The justification for this legislative change from the earlier 1965 Forest Code was the need to transform restoration into a financially-viable land use (Brancalion *et al.* 2012), which compensates farmers for the opportunity costs of foregone agricultural land use. Here, we draw on results from experimental studies at three sites across the Brazilian Atlantic Forest to rigorously assess the impacts of incorporating exotic eucalypts as a transitional stage in tropical forest restoration on aboveground biomass accumulation, native woody species regeneration, and costs. This information is important to evaluate the ecological and financial viability of this novel legal norm and its potential for dissemination to other global regions to leverage tropical forest restoration.

Materials and Methods

Experimental sites

We established experimental plantings in three municipalities distributed across the eastern portion of the Atlantic Forest (Site 1: Aracruz-Espírito Santo, Site 2: Mucuri-Bahia, and Site 3: Igrapiúna-Bahia; **Table S1**, **Fig. 1**) as a joint effort of the Atlantic Forest Restoration Pact, two eucalypt pulp companies, and one conservation NGO to develop new forest restoration models with the objective of offsetting implementation costs and providing income to farmers. We established and compared two experimental treatments at each site: i) diverse plantations of native species: 23-30 species of native non-pioneer trees intercropped with 9-10 species of native pioneer trees (hereafter "native" treatment); ii) mixed plantations of native species and eucalypts: the same 23-30 species of native non-pioneer trees intercropped with eucalypts in equal proportions of eucalypt and native non-pioneer species ("mixed" treatment; **Table S1**). Native non-pioneer trees were mostly composed of valuable timber species, which could potentially be harvested by farmers in long rotation cycles to further contribute to the financial viability of restoration. We employed a random block design with five (site 1), four (site 2) and six (site 3) blocks (**Table S1**). Sites 1 and 2 were planted at 3 × 3 m spacing (1,111 trees ha^{-1}; plot size 2,160 m^2) and site 3 at 3 × 2 m spacing (1,666 trees ha^{-1}; plot size 1,080 m^2); in all sites, we intercropped two consecutive lines of each group of species (*i.e.,* eucalypts, native pioneers, and native non-pioneers).

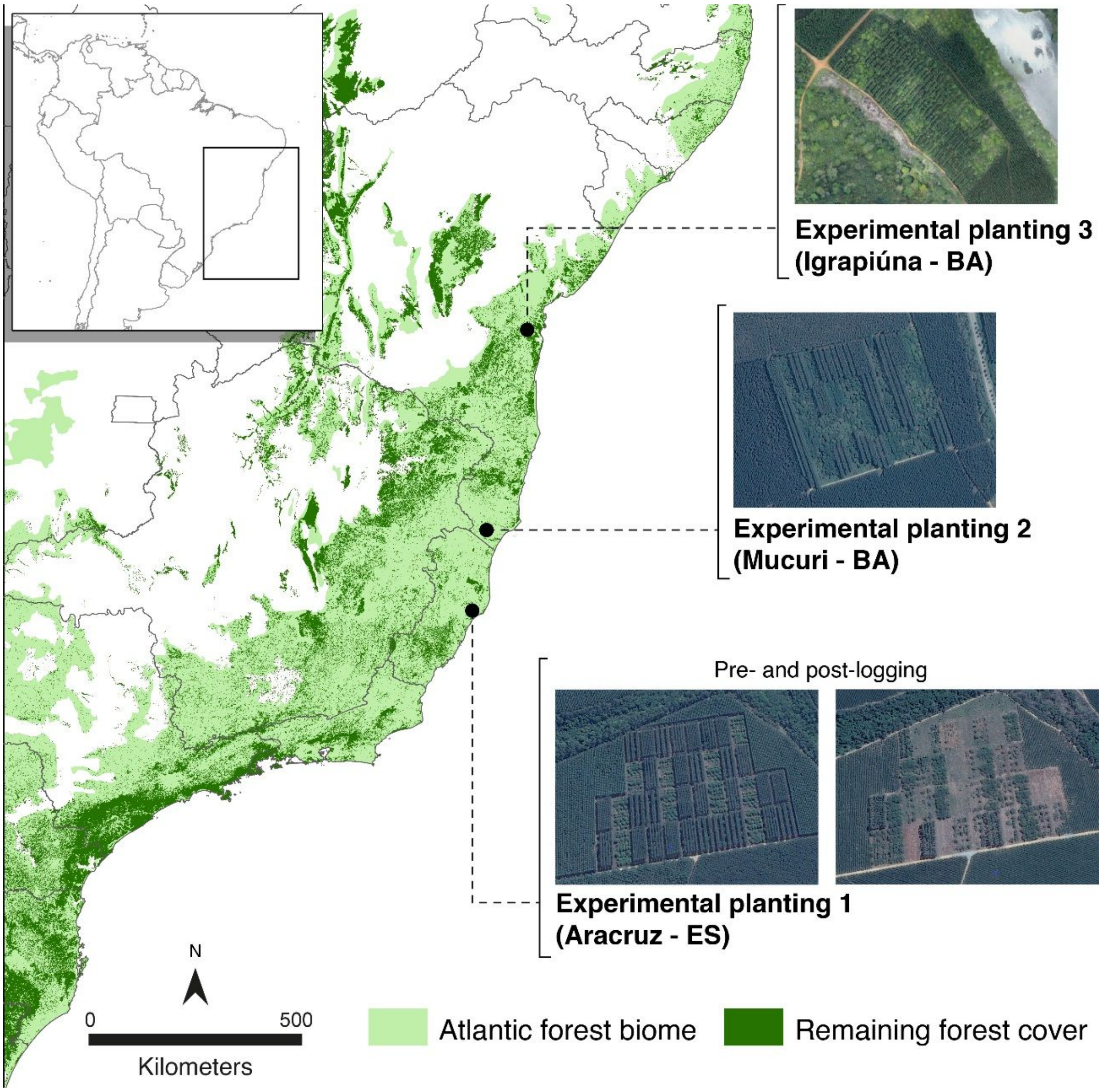

Figure 1. Study sites within the Atlantic Forest of Brazil. Black lines in Atlantic Forest map indicate state boundaries. See Table S1 for biophysical and experimental site details. Other treatments were tested in these sites and can be seen in the images (e.g. eucalypt monocultures, intercropping eucalypts and native species in single lines), but these treatments are not discussed in this paper.

We logged eucalypt trees in all mixed plantation plots at site 1 with a harvester and forwarder after 57 months, and logged all eucalypt trees in half of these plots (six harvested and six unharvested) in site 3 with chainsaw and animal traction after 45 months; mixed plantations have not yet been harvested at site 2 because it is being managed for a longer rotation cycle. We left unharvested plots at site 3 to compare the longer-term impacts of maintaining versus logging eucalypts on the further development of planted native trees and natural regeneration. We employed a reduced impact logging approach in order to minimize logging impacts on planted native trees and natural regeneration.

Data collection

Aboveground biomass accumulation and growth of planted non-pioneer trees

We measured the DBH and height of all planted native trees and eucalypts in the effective area of experimental plots in site 1 (pre-logging: 38, 51 and 57 months; post-logging: 83 months), site 2 (pre-logging: 48 months) and site 3 (pre-logging: 31 and 43 months; post-logging: 53, 60, and 84 months; **Fig. S1**). We estimated native tree aboveground biomass (AGB) 4-5 yr after planting using an equation developed for 5-yr old restoration plantings in the Atlantic Forest (Ferez *et al.* 2015), and calculated eucalypt AGB with an equation developed specifically for eucalypt stands in the study region (Rocha 2014). In the native plantations, we calculated the AGB of pioneer and non-pioneer trees separately in order to assess the differential impact of eucalypts and native pioneers on the growth of native non-pioneer trees.

Regeneration environment and woody species regeneration

We assessed the light environment and invasive grass cover in the plantation understory right before (Site 1: 57 months; Site 3: 43 months) eucalypt logging, and the light environment immediately following and 7 (Site 1) to 12 (Site 3) months after eucalypt logging (**Fig. S1**). We did not take natural regeneration measurements in site 2 because the company in charge of maintaining the site inadvertently sprayed glyphosate in the plantation understory to control grasses, a standard practice in eucalypt plantations, which also killed native regenerating trees; moreover, since the site is being managed on a longer-term rotation, we could not take post-harvest natural regeneration data.

We estimated light availability using two methods due to different weather conditions at the sites. In site 1, where open sky days predominated during the data collection period, we measured photosynthetically active radiation from 11 to 13h in the plantation understory and outside the plantation with a ceptometer AccuPAR LP-80 (Decagon Devices Inc., 1999) and calculated the leaf area index (LAI). In site 3, where cloudy days predominated during the data collection period, we measured the red:far red ratio in plantation understory with a Skye SKR 110 sensor (Skye Instruments), which captures radiation between 660 and 730 ηm wavelengths and does not require measurements in open areas; lower red:far red ratio indicates reduced diffuse transmittance through a more closed canopy (Capers & Chazdon 2004). We regularly distributed ten (Site 1) and six (Site 3) 2 × 2 m quadrat subplots in each experimental plot and visually estimated invasive grass cover (mostly *Urochloa decumbens* (Stapf) R.D. Webster) according to five classes (0, 25, 50, 75, and 100% approximate cover). We then identified and quantified all spontaneously regenerating tree species individuals (height ≥50 cm) growing within the subplots used for grass cover measurements, prior to logging (Site 1: 57 months; Site 3: 43 months) and 3-4 years after post logging.

Logging impacts on planted non-pioneer trees

We evaluated the damages of eucalypt logging on planted non-pioneer species in Sites 1 and 3 right after logging based on a methodology adapted from Sist and Nguyen-Thé

(2002), through which trees were classified as with or without the trunk broken, and with or without damages (damages on tree crown, trunk/bark, and/or bole inclination). We assessed if broken or damaged trees survived seven months after logging, based on the presence of living leaves of new sprouts.

Data analysis

Aboveground biomass accumulation and growth of planted non-pioneer trees

We compared the total AGB and the AGB of non-pioneer species between mixed and native plantations at the pre-harvesting stage 4-5 yr after planting at all three sites. AGB stocks were compared by independent t-tests as data showed normality and homoscedasticity. To compare the growth of planted non-pioneer trees with and without eucalypts, and before and after eucalypt logging, we used linear mixed-models following a model-building approach in order to detect and prevent heteroscedasticity and dependency (Zuur *et al.* 2009). Models were fitted in R using *lme* function in the *nlme* package (Pinheiro *et al.* 2018), using *varPower* and *corAR1* model options when necessary. We used basal area of non-pioneer trees as the response variable, time and treatment as fixed factors and time factor and individual identity as random variables in our mixed models (for more details, see Annex 1). Then, we analyzed how non-pioneer trees responded after eucalypt logging at two sites by comparing plots where eucalypts were logged and areas where non-pioneer trees were growing with native pioneer trees. We compared the basal area increment (difference between the basal area of the pre- and post-logging inventories) between treatments with Welch t-test, since data showed normal distribution but unequal variances.

Regeneration environment and woody species regeneration

The leaf area index (Site 1) and red:far red ratio (Site 3) data were compared between treatments and along time by mixed model approach and paired t-tests. As consequence of the frequent number of subplots with zero values of grass cover, we employed a Zero-Inflated Mixed Model approach (Zuur *et al.* 2009) with the function *zeroinfl* (Zeileis *et al.*, 2008) of *pscl* package (Jackman 2010), using the treatments and the light environment variable as fixed factors in the models. We compared the rarefied species richness and species composition similarity of saplings regenerating in the understories of native and mixed plantations, prior to and after eucalypt logging (Fig. S1). In site 3, we also included unlogged plots of mixed plantations, which allowed us to infer the persistence impacts of eucalypts on native species regeneration.

We compared native species richness through rarefaction curves based on sample-sizes with 95% confidence intervals using the R package *iNEXT* (Hsieh, Ma & Chao 2016), and composition similarity according to the Chao-Jaccard similarity index. We compared the abundance of regenerating native species through Poisson Generalized Linear Mixed Model (GLMM), following a model construction approach (Zuur *et al.* 2009), using *glmer* function from *lme4* package (Bates *et al.* 2015) and post hoc test with *lsmeans* package (Lenth 2016), where time and treatment were fixed factors and plot ID as random factor (for more details, see Annex 1).

Financial calculations

We quantified plantation implementation (site preparation, seedling acquisition, fencing, tree planting) and maintenance (weeding, control of leaf-cutter ants, and sequential fertilization) costs based on the prices of services and materials supplied by professional restoration companies near Site 1. We assumed the costs of Site 1 Aracruz region to be the same as for the other sites, an assumption justified by a large-scale study showing similar costs of restoration management practices across in Brazil. We quantified the differential seedling costs of the two treatments; but we did not quantify the labor and inputs costs of mixed and native plantations separately, although mixed plantings should have lower weeding costs due to faster canopy cover.

We applied a timber price of harvested trees (US$ 28.41 m^{-3}) and discounted logging and transport costs (US$ 6.35 m^{-3}), for the Site 1 region (Silva 2012; Brazilian-Tree-Industry 2015), to calculate total revenue. Timber production was evaluated based on direct harvesting of eucalypts in two sites (Site 1: 100.38 m^3 ha^{-1}, Site 3: 174.08 m^3 ha^{-1}) and estimated in Site 2 based on the relationship between basal area and wood harvested obtained in Site 1 and applied to the forest inventory of Site 2 (93.72 m^3 ha^{-1}). The revenue obtained from eucalypt logging in experimental plantings was calculated based on the Net Present Value, assuming the financial parameters of: i) R$1.00=US$0.3131; ii) inflation of 1.06 (2011-2014) and 1.11 (2015), based on the Broad National Consumer Price Index - IPCA (www.bcb.gov.br/pec/Indeco/Ingl/indecoi.asp); and iii) basic interest rate of 11% for 2014 (www.bcb.gov.br/Pec/Copom/Port/taxaSelic.asp).

Results

Aboveground biomass accumulation and growth of planted trees

Aboveground biomass of mixed plantations was approximately nine times greater than native plantations, mostly as consequence of the rapid growth of eucalypts (**Fig. 2**). These results were accompanied by a slight, but significant, reduction in the AGB of non-native pioneer trees in two experimental sites (**Fig. 2**).

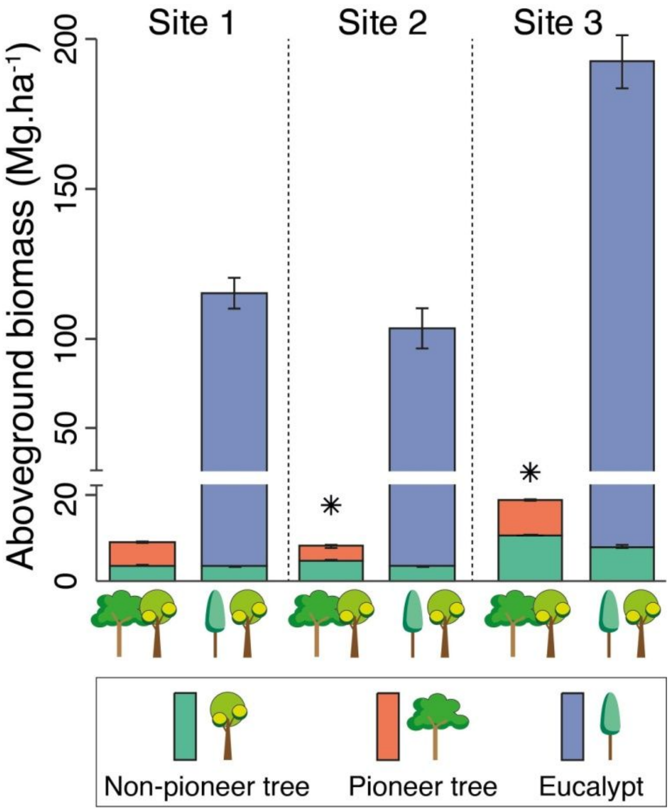

Figure 2. Aboveground biomass (AGB) accumulation in experimental restoration native and mixed plantings. Total AGB was higher in mixed plantations with eucalypts in all sites, and asterisks indicate that AGB of non-pioneer trees was significantly higher without eucalypts (t-tests, $p < 0.05$) in two sites. Error bars represent 95% confidence intervals.

In Site 1, the basal area of non-pioneer species showed similar increases across treatments over time ($F_{1,58}$ =3.33 , p = 0.07; treatment × time interaction $F_{1,58}$ = 5.31, p = 0.02) so basal area in both native and mixed plantations was similar at the last inventory (t_{11} = 0.672, p = 0.98; **Fig. 3A**; **Table S2**). In Site 3, the basal area of non-pioneer species increased faster in native plantations during the experiment (slope estimate ± SE: native = 0.102 ± 0.03; mixed logged = 0.042 ± 0.02, and mixed unlogged = 0.044 ± 0.02; treatment × time interaction $F_{1,46}$=8.94, p <0.005; **Fig. 3B**), which resulted in a 94% higher basal area seven years after planting in the native compared to mixed plantation ($t_6 = 4.318$, $p<0.005$). Eucalypt logging did not affect basal area increment in mixed plantations ($t_{10} = 0.868$, $p = 0.406$).

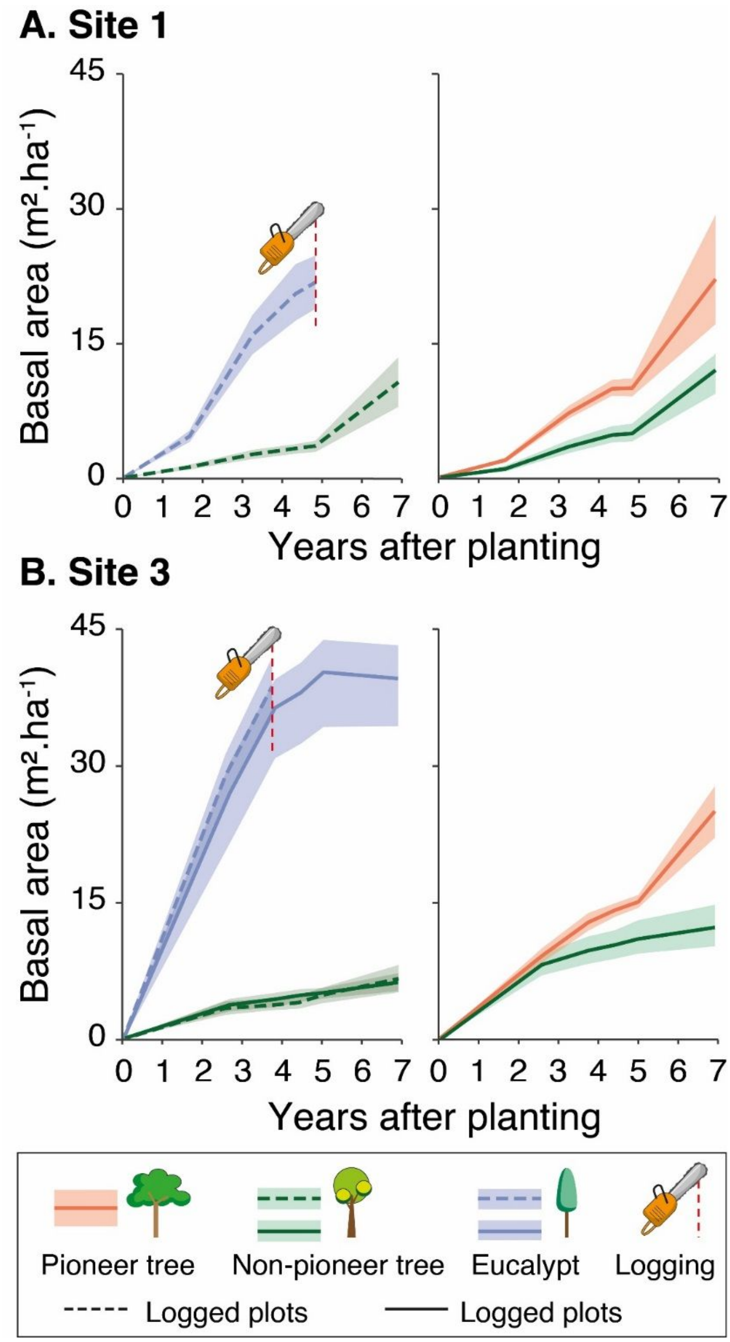

Figure 3. Temporal variation in basal area of species groups in experimental restoration mixed (left) and native plantings (right), submitted or not to logging. Shading represents 1 SE.

Logging impacts on planted non-pioneer trees

Logging impacts were higher in site 3 (45.4% of non-pioneer trees), where eucalypt was logged with chainsaw, than in site 1 (13.2%), where logging was done using a harvester machine (**Table 1**). Nonetheless, mortality was very low in both sites after seven months (**Table 1**), since most broken and damaged trees resprouted following logging damage.

Table 1. Impacts of eucalypt logging on planted non-pioneer trees in mixed plantations, and mortality of impacted trees seven months after harvesting

Study Area	Broken trees (%)	Broken trees mortality (%)[1]	Damaged trees (%)	Damaged trees mortality (%)[1]
1	0.0 ± 0.0	0.0 ± 0.0	13.2 ± 1.8	0.0 ± 0.0
3	16.9 ± 3.4	2.6 ± 0.5	45.4 ± 4.8	0.7 ± 0.5

[1]percentage of dead trees in relation to the total number of alive trees before logging

Regeneration environment

The leaf area index of native and mixed plantations was similar in site 1 prior to logging ($t_{7.1}$ = 1.03; p = 0.38; **Fig. 4A**). Eucalypt logging reduced LAI by nearly a third in mixed plantations (t_9 = 11.95; p < 0.001; **Fig. 4A**), but the growth of the remaining planted and regenerating native trees more than tripled the LAI of logged plots and reached 84% of pre-logging values 7 months after logging (**Fig. 4A**). In site 3, red:far red ratio was lower (i.e. canopy cover was higher) in native plantations prior to logging ($F_{2,429}$ = 132.88; p <0.001; **Fig. 4B**, **S2**). Eucalypt logging showed a similar trend in site 3 (~30% increase in red:far red ratio values; t_{143} = 25.97; p <0.001; **Fig. 4B**). A year post logging, the remaining native trees had reached 85% of red:far red ratio values of unlogged mixed plots and 68% of native plantations values, yet logged mixed plots had the highest red:far red ratio values at this time ($F_{2,429}$ = 426.5; p <0.0001**;** **Fig. 4B**). Invasive grass cover was low in both sites (Site 1: ~10%; Site 3: ~7%) and did not differ between treatments prior to logging (Site 1: |Z|<1.44; Site 3: |Z|<0.53; p > 0.05).

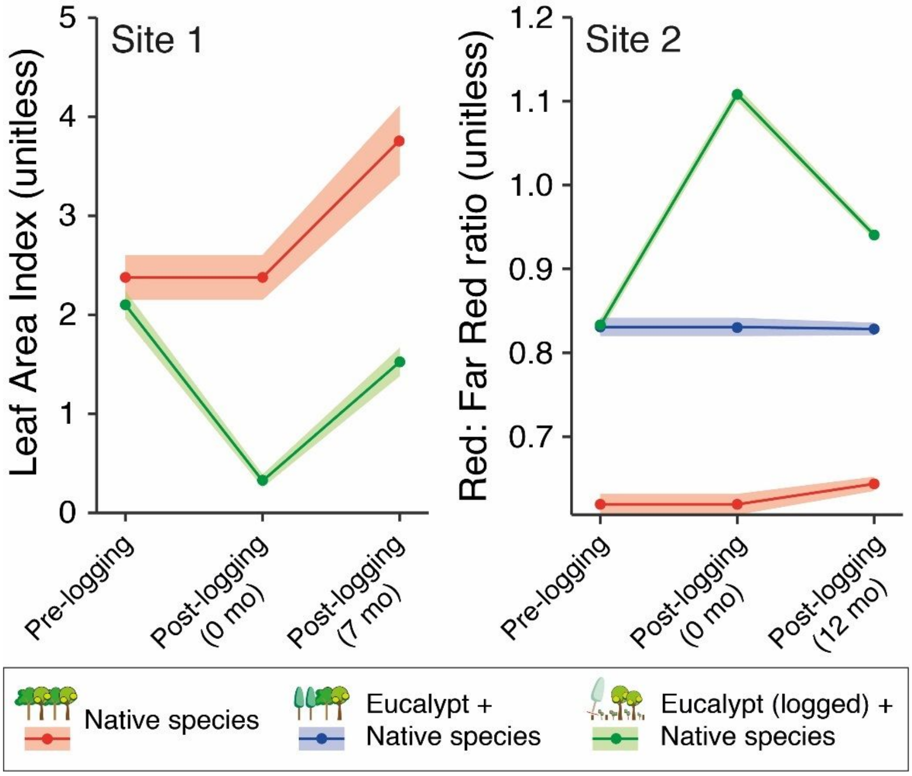

Figure 4. Temporal variation of light environment in the understory of experimental restoration plantings of native and mixed plantations, submitted or not to logging. Shading represents 1 SE.

Regeneration of native woody species

Rarefied species richness and composition of native woody species that colonized the understory of native and mixed plantations were similar in the pre-logging period (Site 1: Chao-Jaccard similarity: 0.75; **Fig. 5A**; Site 3: Chao-Jaccard similarity: 0.95; **Fig. 5B**) with twice as many species at site 3 compared to site 1. Rarefied species richness doubled and tripled in sites 1 and 3, respectively, in the post-logging period, but did not differ among plantation types within each site (**Fig. 5**). We did not observe a single regenerating eucalypt seedling in either site pre- or post-logging. In site 1, the abundance of regenerating native species was higher in native plantations in the pre-logging period, but was similar at the post-logging period (Table S3), as consequence of a slight abundance decrease in native plantations and increase in mixed plantations between periods (slope estimate ± SE: Site 1: native = -0.28 ± 0.25; mixed = 1.55 ±0.24; treatment × time interaction $|Z|$=5.33, p <0.001; Table S3). In site 3, the abundance of regenerating native species was similar in treatments in the pre-logging period, but was higher in native plantations in the post-logging period, when logged and unlogged plots did not differ (Table S3). We observed a slight increase in the abundance of regenerating species in native plantations and a decrease in mixed plantations (native = 0.06 ±0.09; mixed logged = -0.35 ± 0.11, and mixed unlogged = -0.29 ±0.11; treatment × time interaction $|Z|_{logged} = 2.79$, $p = 0.005$, and $|Z|_{unlogged} = 2.42$, $p = 0.02$; Table S3).

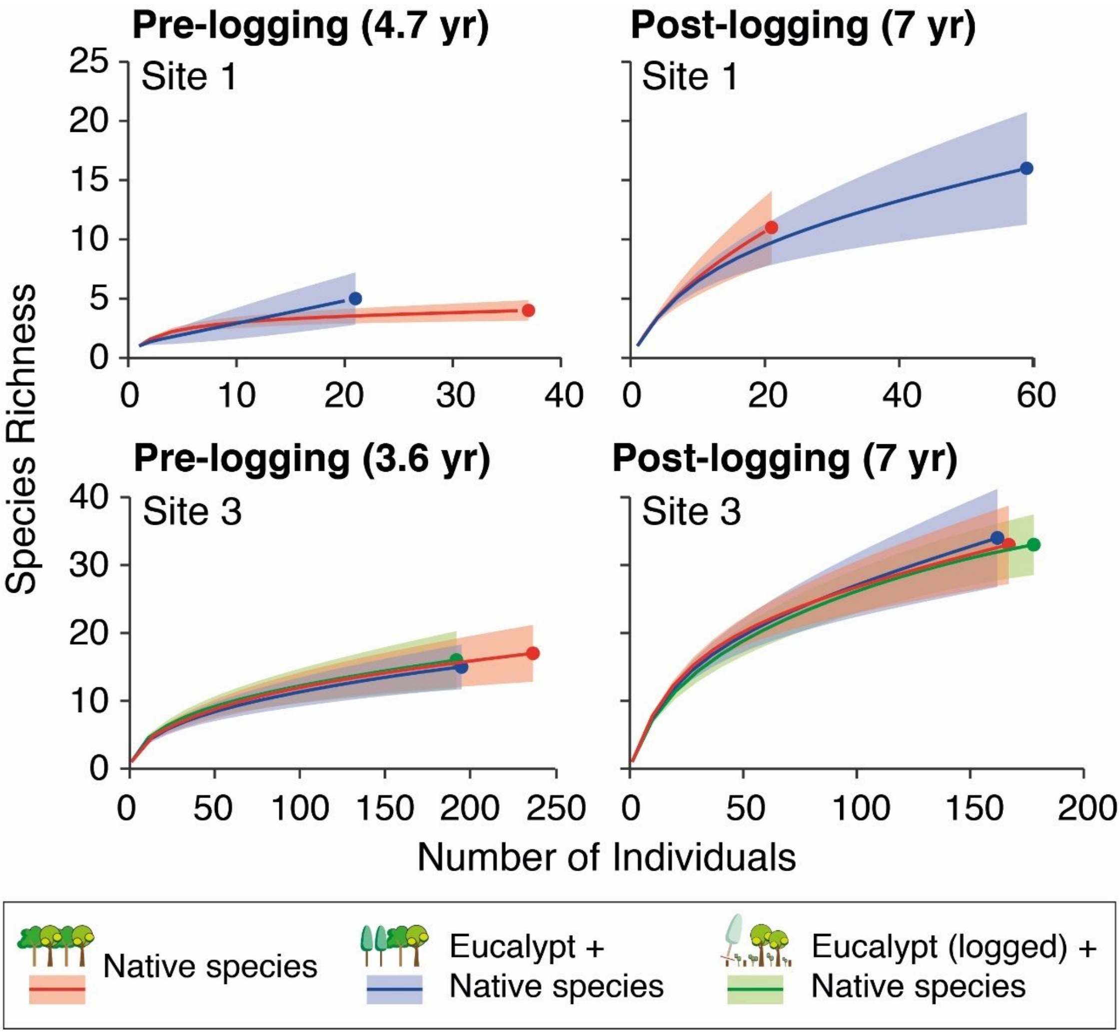

Figure 5. Rarefied species richness of naturally regenerating native woody species in native and mixed restoration plantings with or without eucalypt logging. Shading represents 95% confidence intervals.

Financial assessment of eucalypt logging

Wood production in mixed plantations with eucalypts helped to offset the high implementation and maintenance costs (\$3,360 ha^{-1}). Eucalypt harvesting in 4-5 yr old experimental plantings yielded 100 (Site 1), 94 (Site 2), and 174 m^3 ha^{-1} (Site 3) of roundwood for pulp, firewood or fencing poles (DBH 15-25 cm), compensating for 46.6 (Site 1), 44.00 (Site 2), and 75.3% (site 3) of total restoration implementation costs 4-5 years after planting (Table S4).

Discussion

Our results show that mixing plantations of eucalypts and native trees is a promising restoration strategy to help offset restoration implementation costs without undermining the ecological outcomes. The growth of native non-pioneer trees was not affected (1 site) or slightly reduced (2 sites) by eucalypts prior to logging despite the greatly enhanced biomass production of mixed plantations. Moreover, the richness of regenerating native woody species was not reduced by eucalypts either before or after eucalypt logging, yet the abundance of regenerating native species was higher in native plantations in sites 1 (pre-logging) and 3 (post-logging).

The most evident difference between native and mixed plantations was the short-term difference in AGB accumulation. With nearly nine times higher AGB stocks prior to logging, mixed plantations clearly demonstrated the value of integrating eucalypts as a transitional phase in restoration if wood production is one of the expected outcomes (Amazonas *et al.* 2017; Lamb 2018). The fact that the impressive biomass accumulation of eucalypts did not strongly reduce the growth of planted native non-pioneer trees may be due to the naturally slow growth of this group of species (Chazdon 2014) and their adaptation to tolerate low to medium light conditions (Loik & Holl 1999). We lack plantations of exclusively non-pioneer trees to disentangle competition in these systems.

We had anticipated that the fast growth of eucalypts would result in higher canopy cover and consequently less grass cover than native plantations. In contrast, we found the opposite result for canopy cover in one site and no difference in another, and no impact on grass cover in either site. These unexpected results can be explained by the contrasting architecture of the tree crowns of eucalypts and native species. The eucalypt species used in the experimental plantations have monopodial branching, which concentrate leaves at the top of plantation canopy and result in a leafless midstory (Almeida *et al.* 2019). On the other hand, native plantations usually have branches and leaves throughout all the forest vertical strata to maximize light absorption by species with different ecophysiological behaviors and niche requirements (Sapijanskas *et al.* 2014). The shade levels in both plantations types appeared to be sufficiently high to prevent grass regrowth in the understory, a major barrier for restoration success in the Atlantic Forest region.

A valid concern about interplanting eucalypts with native species is that the impacts of falling trees and dragging logs could largely destroy the native non-pioneer trees interplanted with eucalypts and the abundant natural regeneration of the understory. In fact, the visual impression right after logging was that all regenerating individuals were destroyed in eucalypt planting lines, where logging impacts were concentrated (**Fig. S3**). In site 3, nearly half of planted non-pioneer trees were damaged by logging; but most broken trees resprouted and damaged trees survived seven months after logging, resulting in negligible mortality levels. The species richness of regenerating woody plants was similar between logged mixed plantations and native plantations a few years after logging, but the abundance of regenerating individuals was reduced in both logged and unlogged mixed plantations in site 3 compared to native plantations. We had expected planted native non-pioneer trees would grow faster in the post-logging period, given that seedling growth is commonly light limited in plantations (Paquette, Bouchard & Cogliastro 2006) and tropical secondary forest (Chazdon *et al.* 1996), but growth post-logging growth rates were similar in logged and unlogged treaments. In site 3, the potential benefits of greater light availability may have been counterbalanced by the higher levels of physical damage of logging to planted native non-pioneer trees.

The lack of differentiation of regenerating communities both in terms of species richness and composition, may reflect the spatial proximity of the plots. Although we used large experimental plots (2,160 and 1,080 m²), compared to those traditionally used in restoration experiments (Shoo & Catterall 2013), seed dispersers may have been attracted to the heterogeneous forest structure and abundant animal-dispersed trees of the experimental site in general (Reid, Harris & Zahawi 2012). This local enhancement of seed dispersal could mask the differential potential of native trees, especially of pioneers, to attract seed dispersers, yet some studies have reported diverse bird communities in the understory of abandoned eucalypt plantations in the Atlantic Forest region (Marsden, Whiffin & Galetti 2001; Lopes *et al.* 2015).

Differences in both aboveground biomass accumulation and natural regeneration were much more strongly affected by site factors than by planting treatment. The nearly three-fold higher tree growth rates at site 3 likely reflect more favorable soil and climate conditions (site 3 vs. site 1: soil sum of bases: 23.81 vs. 1.93 $mmol_c.dm^{-3}$; clay content: 71.4 vs. 20.9%; annual rainfall: 2,191 vs. 1,412 mm; **Table S1**) and less intensive prior land use (extensive pasture vs. intensive eucalypt plantation). The greater species richness of recruits in site 3 may be explained by those factors, as well as higher landscape forest cover (20.8% vs. 6.3%) than site 1. All three factors have been demonstrated to affect the rate of tropical forest recovery in prior studies (reviewed in Holl 2007; Chazdon 2014).

Eucalypt allelopathic effects (Becerra *et al.* 2017), cases of invasion (Tererai *et al.* 2013), reduction in soil moisture (Robinson, Harper & Smettem 2006) and problems with wildfires (Moreira & Pe'er 2018), have been reported predominantly in drier climates. These do not seem to be similarly problematic issues in wetter tropical regions, as suggested by our results and several previous studies in tropical regions that found diverse and abundant regeneration of native species in the understory of eucalypt plantations (e.g. Silva-Junior, Scarano & Cardel 1995; Bremer & Farley 2010; Pryde *et al.* 2015). We did not find any evidence of natural recruitment of eucalypts in our plots. Data from a related study at our sites (Amazonas *et al.* 2017) showed minimal differences in soil volumetric water content in shallow soil layers (up to 1.3 m depth) of ~4.5-yr native, mixed, and eucalypt monoculture plantations. This lack of difference in soil water availability may be due to the fact that most native pioneer species also require large amounts of water to sustain their fast growth (Filoso *et al.* 2017).

As expected, eucalypt logging resulted in a valuable contribution to offset ~45-75% of restoration implementation and maintenance costs. Harvesting eucalypts or other commercially valuable native or exotic trees in restoration could partially overcome the financial barrier for adopting active restoration approaches, which can cost up to ten times more than natural regeneration (Shoo *et al.* 2017), but are needed in many cases due to low site resilience (Rodrigues *et al.* 2011; Shoo *et al.* 2016). Exotic eucalypts can thus become important allies of tropical forest restoration, and their use should be considered within the portfolio of options supported by public and private funding and policies (Catterall 2016). Together, our results suggest eucalypt use as a transitional stage in restoration has a neutral effect on natural regeneration and can help offset restoration costs along with complementary strategies that aim to transform restoration into a competitive land use, like payments for ecosystem services and harvesting valuable native timber species in long rotations (Brancalion *et al.* 2017). Like any novel restoration strategy, this approach must be considered in the context of the ecosystem type and evaluated for localized positive and negative effects prior to large-scale implementation.

Data archive statement: Our data is archived at GitHub (https://doi.org/10.5281/zenodo.2583906).

Author contributions: P.H.S.B. conceived the idea, designed the study, and led the writing. K.D.H. co-led the writing. P.H.S.B. and K.D.H decided on statistical analysis and J.M. conducted them. N.T.A., C.C.S., T.B.S., A.F.M., P.H.S.B., and R.R.R. planned the experiment and collected data. R.L.C. helped to structure and review the manuscript.

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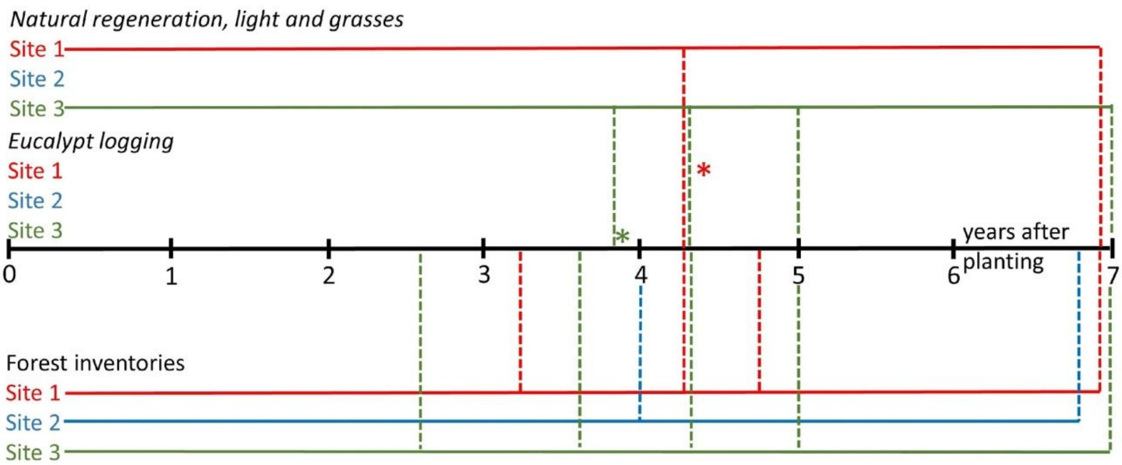

Figure S1. Timeline of interventions and data collection in the three experimental sites.

Fig. S2. Hemispheric photographs of the canopy of native (left) and mixed (right) plantations.

Fig. S3. Overview of the mixed plantation in Site 3 right after eucalypt logging.

Table S1: Biophysical and experimental characteristics of the study sites.

Characteristics	Experimental plantings		
	Aracruz Espírito Santo state	Mucuri Bahia state	Igrapiúna Bahia state
Coordinates	19°49′12″S, 40°16′22″W	18°05′09″S, 39°33′03″W	13°49′0″S, 39°9′0″W
Land tenure	Private	Private	Private
Altitude	41 m	78 m	121 m
Mean rainfall	1,412 mm	1,531 mm	2,191 mm
Mean temperature	23.4°C	23.9°C	25°C
Climate (Köppen classification)	Aw; dry cold winter and a hot wet summer	Af; no dry season	Af; no dry season
Drier period	Feb-Sep	Jan-Apr	Nov-Mar
Soils	Yellow Argisol (Ultisol); sandy/ clayey texture	Argisol; clayvey (40%)	Dystrophic Yellow-Red Oxisol; clayey
Cation Exchange Capacity ($mmol_c.dm^{-3}$)	2.16	1.83	58.64
Sum of Bases ($mmol_c.dm^{-3}$)	1.93	1.43	23.81
Clay (%)	20.9	17.2	71.4
Relief	Flat	Flat	Rounded hills with soft slopes
Native forest cover within a 5-km radius	6.3%	28.3%	20.8%
Experimental design	Random block design; 5 blocks	Random block design; 4 blocks	Random block design; 6 blocks
Treatments*	NE; NN; EE	NE; NN; EE	NE; NN
Date of plantation	July 2011	May 2012	June 2011
Plot size	2,160 m^2	2,160 m^2	1,080 m^2
Plot design	10 lines of 24 trees; two outer rows as border	10 lines of 24 trees; two outer lines as border	15 lines of 12 trees; one outer line as border
Plantation spacing	3×3 m	3×3 m	3×2 m
Number of seedlings within effective plot	120	120	130

Seedlings per hectare	1,111	1,111	1,667
Eucalypt planted	*E. grandis* × *E. urophylla*	*E. urophylla*	*E. grandis* × *E. urophylla*
Native pioneers	10 species	10 species	9 species
Native non-pioneer	30 species	28 species	23 species

* NE= native species + *Eucalyptus*; NN= native species + native pioneers; EE= *Eucalyptus* monoculture

Table S2 –Basal area mean of native non-pioneer species in the last inventory, with confidence limits obtained by a nonparametric bootstrap.

Site	Treatment	Mean basal area (m^2ha^{-1})	Minimum limit	Maximum limit
Site 1	Native	0.0221	0.0179	0.0265
	Mixed logged	0.0281	0.0187	0.0384
Site 3	Native	0.0120	0.00926	0.0153
	Mixed logged	0.00785	0.00624	0.00968
	Mixed unlogged	0.00781	0.00634	0.00959

Table S3. Abundance of regenerating native wood species per plot (mean and minimum – maximum confidence limits by nonparametric bootstrap, 95% confidence interval and 1000 bootstrap resamples).

Site	Treatment	Before logging (50 months)	After logging (83 months)
Site 1	Native	9.25 (7.0 - 11.8)	7 (4.8 - 9.8)
	Mixed logged	2.3 (1.6 - 3.1)	11 (5.3 - 17.7)
Site 3	Native	7.3 (4.6 - 10.6)	8.2 (6.1 - 10.4)
	Mixed logged	5.7 (4.1 - 7.4)	3.9 (3.0 - 4.9)
	Mixed unlogged	6.3 (4.5 - 8.2)	4.7 (3.9 - 5.6)

Table S4: Economic analysis of the potential of harvesting eucalypt timber (4-5 yr rotations) in mixed plantings with native trees to offset per hectare restoration implementation and maintenance costs in the Atlantic Forest of Brazil.

A. Traditional restoration plantings, without eucalypts

Site	Year	Activity	Costs	Revenue	Present Value	Net Present Value	restoration costs offset
all	0	Site preparation	$ -775	$ -	$ -775		
all	0	Planting	$-1,034	$ -	$-1,034		
all	0	Maintenance	$ -232	$ -	$ -232		
all	1	Maintenance	$-1,023	$ -	$ -922		
all	2	Maintenance	$ -310	$ -	$ -251		
all	3	Maintenance	$ -122	$ -	$ -89		
all	4	Maintenance	$ -50	$ -	$ -33		
all	5	Maintenance	$ -40	$ -	$ -24		
all	5				$ -	$-3,360	0%

B. Mixed plantings of eucalypts and native trees

Aracruz	Year	Activity	Costs	Revenue	Present Value	Net Present Value	restoration costs offset
Aracruz	0	Site preparation	$ -775	$ -	$ -775		
Aracruz	0	Planting	$ -928	$ -	$ -928		
Aracruz	0	Maintenance	$ -232	$ -	$ -232		
Aracruz	1	Maintenance	$-1,023	$ -	$ -922		
Aracruz	2	Maintenance	$ -310	$ -	$ -251		
Aracruz	5	Logging and transport	$ -638	$ 2,852	$ 1,314	$-1,795	46.6%
Mucuri	0	Site preparation	$ -775	$ -	$ -775		
Mucuri	0	Plantation	$ -928	$ -	$ -928		
Mucuri	0	Maintenance	$ -232	$ -	$ -232		
Mucuri	1	Maintenance	$-1,023	$ -	$ -922		
Mucuri	2	Maintenance	$ -310	$ -	$ -251		
Mucuri	5	Logging and transport	$ -596	$ 2,662	$ 1,227	$-1,882	44.0%
Igrapiúna	0	Site preparation	$ -775	$ -	$ -775		
Igrapiúna	0	Plantation	$ -928	$ -	$ -928		
Igrapiúna	0	Maintenance	$ -232	$ -	$ -232		
Igrapiúna	1	Maintenance	$-1.023	$ -	$ -922		
Igrapiúna	2	Maintenance	$ -310	$ -	$ -251		
Igrapiúna	5	Logging and transport	$-1,106	$ 4,945	$ 2,278	$ -830	75.3%